THE OHIO JOURNAL OF SCIENCE

VOL. XXIV MAY, 1924 No. 3

GEOLOGIC FACTORS IN ORGANIC EVOLUTION.*

KIRTLEY F. MATHER
Department of Geology, Denison University

INTRODUCTION.

The presidential addresses delivered at the last two meetings of our Academy, that by Dr. Weiss† at Oberlin in 1923, and that by Prof. Osburn‡ in this room in 1922, both dealt with phases of the broad principle of organic evolution. It is my purpose this evening to accept the precedent thus established and speak to you from the point of view of the geologist with reference to certain problems of life development. With an audience including specialists in many scientific departments, an occasion of this sort demands the consideration of general principles or problems in which men of varied scientific interests may unite on common ground. No excuse is needed at the present time for offering the manifold enigma of life development as one of the most important fields now being cultivated by men of science. We approach the subject from many angles, but we inevitably find a common interest there.

Geologic factors in their broadest interpretation would, of course, embrace all the elements which compose the physical environment surrounding life at any time or place. Moreover, it is evident that many elements of an animal or plant association are present as a part of the organic environment solely by permission of geographical conditions. So closely interwoven are the two parts of any environment, the physical surroundings

* Retiring President's Address before the Ohio Academy of Science, April 18, 1924.

† A. P. Weiss, The Aims of Social Evolution; Ohio Journal of Science, Vol. 23, pp. 115–134, 1923.

‡ R. C. Osburn, Some Common Misconceptions of Evolution; Ohio Journal of Science, Vol. 22, pp. 173–192, 1922.

and the associated life, that the influence of the one is scarcely separable from the influence of the other and both alike may be considered as geologic factors. My topic, therefore, might be interpreted as involving a consideration of the role played by environment in the processes of evolution.

How environment operates in influencing successive generations in the evolution process is a moot question, perhaps one of the most important of all the unsolved problems with which we are now engaged. The wise student of evolution is today not nearly so dogmatic in his assertion that acquired characteristics are not inheritable as were many naturalists a few years ago. Most paleontologists have harboured a lingering hope that in some way the characteristics acquired by one generation may leave their impress upon the next generation. The record of the rocks frequently suggests the question, does environment influence the germ plasm and therefore have something to say about the nature of those born into each generation? Or does environment merely select from those born the few who are to survive because of chance adaptation to their surroundings? Although the geologic record inevitably raises that question, it is probable that no certain answer can be deduced from the study of geologic life development. The problem cannot be solved by the paleontologist because what he sees can be rationally explained on either basis. Apparently the solution must await the results of such studies as are now being prosecuted by experimenting biometricians.

Even though the paleontologist must give over the hope of finding the elusive answer to such fundamental questions as these, it is of real value for him occasionally to take stock of his information and to survey the stage upon which the drama of life has been played. The shift of scenes and change of properties has always found quick response from the actors in the play. A review of such responses at certain critical moments in the past, coupled with an attempt to explain them, may help us as we chart the course which mankind may hope to pursue through coming geologic epochs.

GEOLOGIC FACTORS IN THE ORIGIN OF LIFE.

The first appearance of living organisms upon the earth constitutes an event which will always be fraught with the profoundest interest, but which will probably ever be shrouded

in deep mystery. Almost altogether unhampered by facts, one is left free to speculate along many different avenues. Geologists and astronomers seem in general agreement concerning the likelihood that our earth has passed through a juvenile stage of growth by accretion of "planet dust." The Planetesimal Hypothesis of Chamberlin and Moulton, or some modification of that hypothesis, makes a strong appeal to all who have attempted to sketch the evolution of the solar system. Long before the earth had attained its present maturity, its surface conditions would presumably have been favorable for life as we know it today. All available data indicate that ever since the earth was of dimensions comparable to those now possessed by Venus its atmospheric constitution, surface temperatures, light intensity, etc. have been within the range of conditions under which life is known to exist.

It would be expected that no long delay would ensue after the earth became suitable as an abode for life before that opportunity would have been seized and life originated. If such was the case, living creatures have existed on the earth from a date which must be placed far back beyond the dawn of geologic history, long before the oldest known rocks were formed. The surface of the juvenile earth of that early time must now be buried hundreds of miles deep beneath the materials subsequently added to it during the final stages of organization of the solar system. The high temperature and intense pressure of the earth's interior have long since completely altered those ancient surficial rocks beyond any possibility of recognition. The vast eon of time which has since elapsed has effectively obliterated all vestiges not only of the primordial life itself, but of its terrestrial environment as well.

The only safe grounds within which speculation concerning the origin of life is justified are those which imply that the material substances from which living cells were first constructed were previously present among the rocks and minerals of the earth. Frost,* Osborn†, and others have stressed the fact that the chemical elements essential in living protoplasm

* E. B. Frost, The Contribution of Astronomy to General Culture; Journ. Sci. Lab. Denison Univ., Vol. 16, p. 360, 1911.

† H. F. Osborn, The Origin and Evolution of Life, New York, 1918, pp. 45–48, 59–67.

are among the most ubiquitous of all the elements in the universe. All the necessary ingredients were certainly present in the outer shell of the growing earth. The geologic factors involved in the accretion of planetesimal matter upon the earth's surface afforded almost limitless variety of chemical combinations. The Chamberlins,* father and son, have called our attention to the many unstable and highly complex carbides, nitrides, phosphides, etc., present in the meteorites which have reached the earth's surface during recent time. Presumably these are samples of the material added to the juvenile earth during its Formative Eon. Chamberlin† has set forth in a characteristic masterpiece of logical deduction many reasons for the belief that the pulverized and porous surface layer of the growing earth was the most probable environment in which life may have originated. The open spaces at variable depths below the actual surface of the lithosphere must have been filled by the water of the primitive hydrosphere. Except during times of precipitation, the pores in the ground in close proximity to the surface were comparatively dry. Somewhere between the water table and the surface any desired relationship of water, air, and mineral matter could have been found. Here the long, slow process of chemical synthesis, constructing the chain which led eventually to the first protoplasm, is believed to have taken place. Beyond doubt, there were numerous errors in the many trials attempted at different times and places, but opportunity was practically limitless both in time and space. If the requisite minerals were wanting at a critical point in the synthetic processes in one place, somewhere else the proper sequence might be obtained. If at one locality an unfortunate episode of volcanic activity, crustal movement, or planetesimal infall destroyed the delicate balance between the complex hydrocarbon compounds and their surroundings, somewhere else at some other time there would be no such untoward circumstances.

Chamberlin‡ and Osborn§ have both commented on the frequency with which complex hydrocarbon compounds assume the colloidal rather than the crystalline state. It is thus that

* T. C. Chamberlin and R. T. Chamberlin, Early Terrestrial Conditions that may have Favored Organic Synthesis; Science, Vol. 28, pp. 902-904, 1908.

† T. C. Chamberlin, The Origin of the Earth, Chicago, 1916, pp. 252–256.

‡ Loc. cit., pp. 255–257.

§ Loc. cit., pp. 58–59.

the inorganic world simulates i its physical appearance and constitution the organic. More than likely the postulated chemical synthesis was favored by the presence of colloids in the interstices between the grains of the outer shell of that primitive earth. The suggestion has been made that the walls bounding the tiny spaces in the soil anticipated the development of cell walls inclosing the protoplasm of the primitive unicellular plant-animal.

But this is only a part of the story. Life is something more than matter. Living creatures are characterized by vital energy, something about which we really know very little, but something which is absolutely indispensable to every organism. Obviously the material constituents of life were under the sway of geologic factors. Did those same factors also determine the energy content of the ancestral cell? Abundant sources of energy of various kinds were doubtless present at and near the surface of the growing earth. Solar radiance, electrical vibrations, radioactive compounds, chemical reactions, all of these and perhaps other sources of energy were available. It is conceivable that the synthesis of vital energy paralleled in the spiritual realm, if I may use that term in a very broad sense, the synthesis of protoplasmic substance in the material realm. Here the geologic factors are so obscure that it is hardly worth while to attempt any speculation.

Chamberlin* closes his volume on the origin of the earth with the following thought-provoking sentence: "It is our personal view that what we conveniently regard as merely material is at the same time spiritual, that what we try to reduce to the mechanistic is at the same time volitional, but whether this be so or not, the emergence of what we call the living from the inorganic, and the emergence of what we call the psychic from the physiologic, were at once the transcendent and the transcendental features of the earth's evolution." With this conclusion, many geologists are in hearty accord. May it not be that life as we know it is but one manifestation of the mysterious spiritual powers which permeate the universe? The geologic factors assembled in the primitive earth provided an environment within which the spiritual could manifest itself in the material. The form which it should assume may have

* Loc. cit., pp. 261–262.

been largely determined by that environment. At the very genesis of organic evolution the physical environment presented an opportunity and suggested a method for its utilization. The primitive cell was the result.

GEOLOGIC FACTORS IN THE EVOLUTION OF MARINE INVERTEBRATES.

It is a far cry from that hypothetical first cell, the original primitive plant-animal, to the splendid array of widely deployed marine invertebrates which are recorded in the rocks of the Cambrian period. The record of that tremendous transition is almost entirely lost. The rocks of Archeozoic and Proterozoic age, the first two great eras of known geologic time, can scarcely be expected to reveal the secrets which we would like to know. But the succeeding Paleozoic era witnessed what seems to have been the greatest progress and most significant achievements of marine invertebrates. Dynasties like the trilobites reached their climax and declined almost or quite to disappearance. Organic mechanisms peculiarly devised for efficient locomotion were perfected by a vast multitude of diverse creatures. Sense organs of great usefulness were consummated by the representatives of numerous invertebrate orders. Protective devices of shell covering or other structures reached a superiority which has never been excelled. At the close of the era the assemblage of marine invertebrates was far superior in every way to the ancestral types who had embarked upon the Cambrian seas. Were there factors in the Paleozoic environment which could have been responsible for that remarkable progress?

It happens that our knowledge of Paleozoic geography and history is unusually complete. During that long interval of time the eastern half of North America was close to sea level. Successive oscillations of level from time to time changed the relations between land and sea so that great shallow embayments crept inward from the margins of the continent, inundated vast areas in what are now the eastern states, and later withdrew to the very margins of the continental platform. Schuchert in his Paleogeography of North America* has assembled data concerning the displacements of the ocean

* C. Schuchert, Paleogeography of North America; Bull. Geol. Soc. America, Vol. 20, pp. 427-606, 1910.

strand line during the Paleozoic Era. His quantitative estimates of the inundated areas of North America during successive episodes of marine transgression and continental emergence are, of course, only approximations to the actual facts. The data are by no means accurate and such figures must be held subject to considerable change with increased knowledge. Nevertheless, they give a good idea of the areas involved.

The first inundation of our continent at the opening of the Paleozoic Era apparently did not exceed eighteen per cent of the continental area. It was followed by an emergence during which nearly all of the previously submerged area was above sea level. Shortly thereafter a greater transgression of the sea flooded about thirty-one per cent of the continent, and was followed by an emergence in which more than half of the inundated area became dry land. A quantitative estimate of the succeeding oscillations of land and sea may be succinctly given by quoting the figures for each of the stages which Schuchert has reported on his paleogeographic maps. The successive areas of inundation are as follows: 21%, 12%, 23%, 12%, 57%, 10%, 40%, 5%, 35%, 5%, 35%, 20%, 25%, 5%, 13%, 7%, 27%, 3%, and 1% of the present land area. Apparently these oscillations of the shallow continental seas were among the most important factors contributing to the evolutionary processes. The differences in the figures give a fairly accurate impression of the differences in area available for shallow water life. Times of sea advance and marine transgression were characterized by what has frequently been called expansional evolution. The area available for life was constantly increasing; food supplies were abundant; competition was not severe. Marine invertebrates deployed with utter abandon; every possible experiment was tried; new varieties and species appeared, almost without number. Times of continental emergence were marked by restrictional evolution. The area available was constantly diminishing; living creatures were crowded into ever closer proximity one with another; food supplies were more and more insufficient. The struggle for existence became more acute; the many experiments which had been tried during the luxurious ease of the advancing seas were now appraised and tested. Not only were the decidedly unfit creatures blotted out of existence, but in very truth only the fittest survived. The oscillations of the strand line occa-

sioned pulsations of life. Episodes of expansional and restrictional evolution succeeded one another with monotonous regularity.

Another geologic factor worked in close harmony with the changing area of the shallow sea. Advancing seas invaded each continent from several points of the compass contemporaneously. Embayments like Hudson Bay and the Baltic Sea crept in toward the center of the land areas. For long intervals these embayments were more or less completely isolated one from another. In the main, the Paleozoic seas were probably fairly uniform in temperature, but probably differed materially in salinity and turbidity. A particular embayment, therefore, might be hospitable to certain species such as are found among the molluscs, but at the same time inhospitable to other animals like the corals or the crinoids. Isthmian or other barriers from time to time may have effectively prevented the invasion of an embayment by many forms of life inherently suited to its conditions, and thus have isolated its local population from foreign immigration. For these and other reasons, provincial faunas characterized many Paleozoic epochs.

Each province had its own assemblage of plants and animals, set in a physical environment more or less peculiar to itself. In an attempt to cope with its own special problems, each phylum would perfect its own adaptations. Equilibrium within the province would be attained. Creatures favorably adapted to the local situation would develop. Continued transgression upon the land at many times resulted in the coalescence of hitherto isolated seas. An embayment from the Mackenzie valley, extending southward across Iowa into Illinois, might there become confluent with an embayment from the Gulf of Mexico, extending northward across Mississippi and Tennessee and reaching likewise into Illinois. As a rule, at the climax of sea transgression there was much commingling of the waters of previously separated gulfs and bays. The result is obvious. Provincial faunas mingled with each other and invaded territories from which they had earlier been barred. Life quickly assumed a cosmopolitan aspect as the old barriers were broken down. Again there was abundant opportunity for appraisal of results. Experiments which had proved successful in one embayment were now compared with the best that had been

achieved in another province. The creatures selected in the earlier elimination trials were now pitted against each other in the championship meet. The cosmopolitan type would be characterized by the best possible selections from the many provincial units.

This shifting emphasis from provincial to cosmopolitan faunas must frequently have coincided with the change from expansional to restrictional evolution. The two factors were closely allied. Together they must have contributed tremendously to the sifting processes. The earlier part of an ideal period of the Paleozoic Era would be marked by slowly advancing seas and expansional evolution. The middle of such a period would witness the climax of expansional development and the mingling of provincial faunas to provide the cosmopolitan type. During the later part of the period, retreating seas would carry toward the continental margins the dwindling remnants of the cosmopolitan faunas. These were times *par excellence* of testing and appraisal. Such pulsations as these in environment and life seem to have provided both the necessity and the opportunity for progressive development among marine invertebrates.

The case is particularly clear for animals of that type in the Paleozoic seas, but it is apparent that similar geologic factors have contributed toward the progress of many organisms at all times. Nature thus provides opportunity for the "ceaseless urge" within the organism to experiment with all possible methods of achieving success. Then come the times of testing, when the results of these numerous experiments are weighed in the balance, one against the other. Here is one of the most significant contributions which geologic factors have made to organic evolution.

GEOLOGIC FACTORS IN THE EVOLUTION OF FISHES.

The first known record of vertebrate life is contained in rocks formed during the second period of the Paleozoic Era. The record is a fragmentary one, but it indicates creatures ordinarily interpreted as primitive fish-like forms. The relics are, however, so obscure that they do not give much of a clew to the solution of the problem concerning the origin of vertebrates. In the present inquiry, however, we are not concerned with the missing link between the first vertebrates and their

invertebrate ancestors. Rather we are interested in the environment which favored the development of the higher type of life. Chamberlin* has again given us the advantage of his clear perception of the factors involved. He calls attention to the characteristic distinction between the body form of fishes and that of most other aquatic creatures. He suggests that it is this body form, presumably devised in response to a particular environment, which is the real achievement of these most lowly vertebrates.

To summarize his conclusions, it may be stated that the geologic record contains strong implications that fishes did not originate in the sea. The fragmentary record above referred to is contained in rocks which have been interpreted by many observers as deltaic in nature. The fragments of fish teeth, plates, and bones embedded in the muds and silts, presumably had been transported down a river and thus suffered considerable attrition before they came to rest. The first record of marine fishes, occurring near the close of the next succeeding geological period, decisively indicates long antecedent evolution to account for the wide deployment into diverse orders which had already been accomplished. The complete absence of all ancestral types from the richly fossiliferous marine strata of the earlier Paleozoic periods may be explained only in two ways. Either fishes had been developed in the waters of the land or in some remote and at present altogether unknown sea. Most paleontologists incline to the former view.

"There is only one conspicuous type that is facilely suited to free life, independent of the bottom, in swift streams, and that is the fish-form. The form and the motion of the typical fish are a close imitation of the form and motion of wisps of water-grass passively shaped and gracefully waved by the pulsations of the current. The rhythmical undulations of the lamprey which perhaps best illustrates the primitive vertebrate form, and is itself archaic in structure, are an almost perfect embodiment in the active voice of the passive undulations of river confervæ. The movement of the fish is produced by alternate rhythmical contractions of the side muscles, by which the pressure of the fish's body is brought to bear in successive waves against the water of the incurved sections. In the

* T. C. Chamberlin, On the Habitat of the Early Vertebrates; Journ. Geology, Vol. 8, pp. 400–412, 1900.

movement of a rope of vegetation in a pulsating current, it is the pressure of the pulses of water against the sides of the rope that give the incurvations. The two phenomena are natural reciprocals in the active and passive voices.

"The development in the fish of a rhythmical system of motion responsive to the rhythm impressed upon it by its persistent environment and duly adjusted to it in pulse and force, is a natural mode of neutralizing the current force and securing stability of position or motion against the current, as desired. Beyond question, the form and movement of the typical fish are admirably adapted to motion in static water and that has been thought a sufficient reason for the evolution of the form, and so possibly it may be, but fishes in static water have not as extreme lateral flexibility as have those of running water."*

This very logical explanation of the development of fishes as a response to the environment afforded in swift-flowing streams is of course quite hypothetical. In the present state of knowledge, we have no data adequate either to prove or disprove the theory. It nevertheless opens up a stimulating trend of thought and is in harmonious alignment with deductions made at various other strategic points in life development. Apparently, here as elsewhere, the geologic factors not only set a problem for life to solve, but also whispered a suggestion as to the method of solution.

GEOLOGIC FACTORS IN THE RISE OF TERRESTRIAL VERTEBRATES.

The emergence of air-breathing quadrupeds from the aquatic environment in which live the gill-breathing and finned fishes constitutes one of the most dramatic events along the road leading toward man. Apparently that event occurred shortly after the middle of the Paleozoic Era, for in the later Paleozoic rocks there are abundant footprints and frequent skeletons which indicate the presence of amphibians and reptiles.

Barrell has made a critical study of the geologic factors involved in this particular episode of organic evolution. From his own summary of his paper,† entitled "The Influence of

* T. C. Chamberlin, loc. cit., pp. 407–8.

† J. Barrell, Bull. Geol. Soc. America, Vol. 27, pp. 387–436, 1916.

Silurian-Devonian Climates on the Rise of Air-breathing Vertebrates," the following paragraphs may be quoted.

"The amphibians are represented in the later Paleozoic by certain skeletons preserved in the accumulations of coal swamps, but more abundantly by footprints in formations having the character of semi-arid flood plain deposits. As the record is traced backward, the skeletons disappear, and the oldest abundant traces are footprints left in shales and sandstones, chiefly red in color, of Lower Carboniferous age. These are the deposits of rivers which were in the main subject to seasonal shrinkage in markedly semi-arid climates. The footprints lead us back to the habitats of river fishes, the ancestors from whom they sprang. There are here converging lines of evidence that the rise of amphibians came not from the sea, but from the land waters. The exposure of the tidal zone alternately to water and to air had, then, nothing to do with the origin of lungs.

"Having made this study of environments, the argument passes on to an analysis of causes leading to the rise of amphibians. The law of probabilities shows that the directive influence of external factors is necessary to guide the development of old organic structures into combinations of new structures which shall be efficient under a combination of new conditions. Natural selection, although not now regarded as an explanation of most minor organic variations and the development of new species, is nevertheless a broad controlling force which compels development within certain limits of efficiency. What, then, were the causes which controlled the passage of fishes into amphibians? The chief cause is found to have been the nature of Silurian and Devonian climates. The warm and stagnant waters of the dry season compelled those fishes which should survive to make larger and larger use of air. The organic nature of fishes was at that time happily able to vary in pace with the demands of changing environment.

"The evidence is regarded as strong that the air-bladder was originally developed as a supplemental breathing organ, although in modern fishes it has been mostly diverted to other uses. Among certain Devonian fishes, living under more and more strenuous climatic conditions of seasonal dryness, the use of the air-bladder for respiration became essential, and with the diminishing availability of the waters of certain regions the

gills in those species which survived this crisis in evolution became correspondingly atrophied. The amphibians thus arose under the compulsion of seasonal dryness.

"In conclusion, it is noted how the particular method of accessory respiration which was adopted by the ancestors of amphibians was only one of several methods which have been used by fishes. This method of accessory respiration permitted the rise of land vertebrates and determined the future lines of evolution, but another choice of the mode of respiration might have led to more rapid progress—a progress which would, however, have been directed into somewhat different lines."

Barrell thus concludes that "climatic oscillation is a major ulterior factor in evolution." Again, a geologic factor may be observed to play an important directive part in the drama of life development. The necessities imposed upon the organism because of certain peculiarities in the environment formed a problem which was not impossible of solution. The upward step involved in the evolution of amphibians from fishes was occasioned by local and temporary geologic factors. No ultimate goal could possibly have been even fleetingly envisioned by ambitious fishes. To be sure, the successful achievement of air-breathing apparatus permitted later generations of creatures to progress far by numerous subsequent steps, but the future possibilities were not in the least involved in the momentary crisis. Creatures inherently possessing qualifications which made possible the development of primitive lungs were for the moment set in an environment which stimulated that achievement. The result was of far-reaching consequence to all life.

GEOLOGIC FACTORS IN THE ADVENT OF REPTILES.

The outstanding biologic event of the closing Paleozoic periods was the improvement of terrestrial vertebrates until the reptilian stage was reached. The fossil record shows a nearly complete transition between certain amphibians and the more lowly reptilian orders. No such pronounced structural differences as now separate these two classes of vertebrates were present in late Paleozoic time. In its simplest statement, this forward step in life development involved two changes, both of which were necessary to liberate land animals from the necessity of retaining close contact with their ancestral aquatic

environment. In the first place, the individual's metamorphosis from the gill-breathing to the lung-breathing stage must take place sufficiently early in the life history of the creature to be complete by the moment of birth. Otherwise, the young must be hatched in the water. In the second place, the egg must be so constructed as to permit its incubation in the air rather than in the water.

Lull* has interpreted these changes as a response to a climate becoming progressively more and more arid. He suggests "that whereas semi-aridity with seasonally recurring rains impelled amphibian evolution, true aridity with undependable rains making amphibian economy impossible stimulated the evolution of the reptiles." This explanation is in perfect harmony with the known facts concerning the extension of wide desert areas in what are now the southwestern states, at a time which is approximately contemporaneous with the first records of true reptiles. It happens that some of the very oldest reptile remains are found in the Coal Measures of Illinois, in strata whose composition clearly indicates the presence of marshes and swamps of so vast dimensions as to have been possible only in a humid region. These were, however, coincident in time with vast arid deserts at no remote distance toward the south and west, and it might well be expected that the early reptiles soon sent expeditionary forces from their birthplace in the desert to the adjacent humid lands with their greater wealth of food resources.

Case† has made a paleogeographic study of the environment of North American vertebrates in the Late Paleozoic. He concludes from the available data that the development of vertebrate life at that time "emphasizes the changes from a long period of slow evolution in a singularly monotonous environment through a period of rapid expansion in a diversified environment" resulting in the final extinction of most of the life strains involved. "The chief directing influence in the sudden expansion was a decided climatic change, accompanied by physiographic changes, induced by an alteration in the level of the surface of the continent." The Pennsylvanian period was the next to the last in the Paleozoic Era and was

* R. S. Lull, Organic Evolution, New York, 1917, pp. 494, 5.

† E. C. Case, The Environment of Vertebrate Life in the Late Paleozoic in North America, Carnegie Inst., Washington, D. C., pub. 283, 1919.

succeeded by the Permian period. During Early Pennsylvanian time, the geologic factors surrounding North American life were singularly uniform over most of the continent. Apparently there was an equably humid climate; great areas of the continent were approximately at sea level, so that wide marshes and swamps were an almost constant feature of the landscape. The ultimate food supply, vegetation, was abundant in quantity and an enormous number of animals must have found easy subsistence. The air-breathing vertebrates were still in the first stage of their development—the stage of youth, with all its resiliency, flexibility, and readiness to experiment. But amphibian development seems to have been especially slow. Case suggests that the monotony of the environment restricted the progress which might otherwise have been expected. The vertebrate fauna was, however, "accumulating force towards a great radiation to be expressed as soon as the limitations were removed even in a partial degree." This was apparently one of several long periods of stagnation in evolution which were followed by rapid development, an association so frequently noted that Case records his "impression that faunas in periods of stagnation go through a period of preparation in some form for their subsequent radiation."

Toward the end of the Pennsylvanian period, far-reaching physical changes began to make themselves apparent throughout North America. In general, there was a gradual elevation of the land, accompanied by changes to a cooler and less humid climate. Swamps and marshes dwindled to disappearance. Wide sandy wastes extended over large areas in both the eastern and western half of the continent. Red beds appear among the upper strata of the Coal Measures, and throughout Permian time rocks of that nature were the dominant type in most parts of North America. "The fauna, long restrained from any expression of its evolutionary tendencies, full-fed and in the vigor of its youth, responded at once to the change, and new forms appeared so suddenly as to be unheralded in the preserved remains." Reptiles made their appearance in considerable force and promptly took command of the available lands. Their deployment into diverse strains was especially rapid and was no doubt a response to the varied opportunities of the notably diversified environment. The strange and mysterious fin-backed lizards, the graceful, slender, swift-moving *Areoscelis*,

and the efficiently aquatic mesosaurs are suggestive of the products of three of the many lines of evolution which were pursued.

Somewhat similar climatic and physiographic conditions maintained in South Africa at that same period in earth history. There, also, the reptiles took advantage of the congenial surroundings and the new opportunities. Progress was along very similar lines. But at that locality, one reptile strain showed tendencies which foreshadow the evolution of mammals. So far as the fossil record goes, these tendencies are most apparent in the teeth and skulls. We know nothing definite concerning the progress toward the two truly mammalian characteristics, the utilizing of a portion of the energy derived from food to keep the body temperature above that of the surroundings, and the development of mammary glands for suckling the young. It is, however, within the bounds of probability that both of these mammalian characters were anticipated among therapsid reptiles at that time. If so, it was doubtless a response to another climatic change and thus indicates anew the controlling and directing influence of geologic factors.

The progressive diversification of climate during late Paleozoic time reached its climax with the arrival of a great ice age. In fact, the available evidence would indicate that the late Paleozoic glaciation marked *the* great ice age, for its glaciers were considerably more extensive than those of the much more recent glacial episodes which we commonly designate by that proud term. Regardless of comparisons, during this time of early evolution among the reptiles, there were repeated refrigerations of climate which caused ice sheets to invade the margins of the tropical zone in Africa, South America, and possibly elsewhere. It was at this time that mammal-like characters make their appearance among certain of the reptiles. It was shortly thereafter that the first creatures ordinarily interpreted as mammals left their scanty record in the rocks.

Obviously, diversification of climate, aridity here, glaciation there, are recurrent episodes in the later history of the earth. The opportunity which such climatic factors give for progressive development among land creatures has been offered many times, but only at this critical stage in the evolution of life were there amphibians capable of responding to the growing aridity and

thus of developing into reptiles. Only at this time were there primitive reptiles buoyantly youthful, capable of responding to the adversity of progressive refrigeration by developing mechanism for the manufacture and storage of heat within their bodies.

GEOLOGIC FACTORS IN THE RISE OF MAMMALS.

The Mesozoic Era, which followed the Paleozoic, is designated as the "Age of Reptiles" because during that long interval of time, reptiles dominated land, sea, and air. The excellent start which reptiles had made in response to the changing conditions during the closing moments of the Paleozoic Era bore rich fruit in the host of saurians, peculiarly adapted to every conceivable environment, which retained chief prominence throughout Mesozoic time.

But this era is also characterized by the advent and early development of mammals. Fragmentary remains of teeth and jaws, preserved in the rocks formed during the first of the Mesozoic periods, are ordinarily interpreted as indicating the presence of egg-laying mammals of small size and in few numbers. They are beyond doubt the offspring of the therapsid reptiles whose response to the increasing cold of the late Paleozoic glacial epoch foreshadowed mammalian characteristics and blazed the trail for mammalian progress. Although there were considerable fluctuations of climatic and physiographic conditions during Mesozoic time, there were no geographic changes comparable to those which marked the transition from the Paleozoic to the Mesozoic until a somewhat similar transition occurred at the close of the Mesozoic Era. The main lines of evolutionary progress among vertebrates seem to have been blocked out at the very start of Mesozoic time, and were followed with little deviation during its successive periods. The mammals showed a remarkably slow though steady development.

Not a single complete mammal skull, much less a complete mammal skeleton, has yet been secured from Mesozoic rocks. Our information concerning the early progress of mammals is based on fragments of jaws and scattered teeth. These are ordinarily interpreted to mean that about the middle of the era, mammals similar to the marsupials of today were present. These creatures, though viviperous, possess no mechanism

for the long continued nourishment of the embryo within the body of the female. Therefore, the young are born in an extremely immature stage and are for a time carried in a pouch on the abdomen of the female. No relics which can possibly be interpreted as pertaining to placental mammals have yet been found in Mesozoic rocks. The peculiarly archaic appearance of the placentals, whose remains are abundant in the first strata of the next era, accords with the customary conclusion that placental mammals did not appear until the transition between Mesozoic and Cenozoic time.

The reasons for this apparent mammalian reluctance to develop rapidly are quite obscure. In part, their stagnation may be explained as similar to that displayed by the amphibians in the latter part of the Paleozoic Era. Mesozoic climates and geography were not nearly so uniform or static as those of early Pennsylvanian time, but on the other hand they were not nearly so varied and diversified as those which characterize the opening and closing epochs of many eras. Again, the slow progress of mammals has been explained as due to the tremendous overburden of reptilian life which temporarily dominated all vertebrate evolution. In the face of such tremendous odds, the mammals could try no new experiments and may have been quite content with their good fortune in managing to escape complete extinction. Yet, this adverse organic environment would seem a likely stimulus toward progress. What achievements were attained by Mesozoic mammals appear in large part a response to the necessities imposed upon them by their reptilian enemies. Such a typically mammalian characteristic as parental affection must have been stimulated by the necessity of protecting immature young from the depredations of the multitude of carnivorous dinosaurs and other blood-thirsty saurians. Mammalian intelligence, whether instinctive or reasoning, may likewise have been stimulated in a similar way. Frail and puny mammals could escape powerful and huge reptiles only by outwitting their more muscular opponents. Sharp wits rather than sharp claws, quickness of mind rather than quickness of limb, stood the mammals in good stead in those dark ages of reptile strength.

Attention has frequently been called to the fact that the customary food of placental mammals is directly or indirectly supplied by angiospermous vegetation. Nuts and fruits, herbs

and grains, grasses and shrubs, are the basic food resources of all modern animals. None of these were present in any abundance at the opening of Mesozoic time. Although scanty records of plants believed to be primitive angiosperms have recently been found in the late Paleozoic Coal Measures, it is certainly true that angiosperms were not present as a quantitatively important part of the flora until after the middle of the Mesozoic Era. The revolution in the flora which took place at that time did not, however, make any great impress upon terrestrial life. It is hardly possible that the lands upon which angiosperms became numerous were geographically isolated from those upon which the Mesozoic mammals were residing. Rather, it would seem that other conditions than the nature of the food supply determined the slow progress and final arrival of the higher mammals.

Mesozoic mammals were probably more or less omnivorous, with a penchant for the eggs of reptiles and birds. This may have played an important part in the downfall of the dinosaurs and other terrestrial reptiles who were presumably accustomed to depositing their eggs on the warm sands and leaving them unattended to be incubated by the heat of the sun. In any event, the fossil remains of land reptiles are mingled with ever increasing numbers of mammal jaws and teeth in successively higher strata deposited toward the close of Mesozoic time. Then came an abrupt change, a veritable revolution, affecting all the vertebrate population of the earth. The close of the Mesozoic Era is marked by the complete downfall of the reptiles and was soon followed by the advent in great force of the placental mammals. This overthrow of reptile domination cannot, however, be attributed to success on the part of placental mammals in a contest for supremacy with the saurians. Our records indicate that it was not until after the dominant reptiles had disappeared that the placental mammals appeared upon the scenes. If the downfall of the reptiles is to be attributed to the achievement of the mammals, all credit for that successful revolution must be given to the non-placental mammals of the Mesozoic Era. More likely, mammalian depredations constituted only a very minor part of the many factors involved in this significant change.

The close of Mesozoic time was marked by far-reaching physiographic changes which involved the uplift of continents

and the crumpling of strata into vast mountain ranges as well as the initiation of volcanic outbursts on an unusually vast scale. The resulting climatic changes are not known with such fullness as characterizes our knowledge of late Paleozoic climates. There may not have been so sharp a zonal concentration of tropical warmth and polar coolness as today. Yet there is some evidence which indicates that about this time, glaciers were active in British Columbia and Colorado. These may have been in high mountains or on lofty plateaus rather than close to sea level, but nevertheless their presence is significant. In all probability the crustal movements which marked the close of Mesozoic time, like those which closed the Paleozoic Era, were accompanied by marked refrigeration of the earth's atmosphere. By this time the reptiles had passed through their racial maturity and were in racial old age with all that such senility implies. Peculiarly adapted for special environments and special climates, they were unable to change their bodily structures to conform to the needs of new surroundings. Extinction of the dinosaurs, the pterosaurs, the plesiosaurs, and the icthyosaurs was the inevitable result of changing geologic factors. Upon the stage thus vacated the placental mammals promptly appeared and with the opening of the Cenozoic Era they became the dominant type of terrestrial life.

GEOLOGIC FACTORS IN THE EVOLUTION OF TERRESTRIAL MAMMALS.

The evolution of placental mammals upon the various land areas of the several continents gives to the Cenozoic Era the designation, "Age of Mammals." Diversified climates, varied physiographic conditions, and more or less complete subdivision of lands into isolated provinces, all contributed to the wide and rapid development of the higher mammals. Matthew* has assembled a multitude of pertinent facts in his study of the influence of climate upon the dispersal of mammals during this time. Numerous authors have called attention to the obvious influences of environment upon mammalian progress. One illustration will suffice to bring the general principles clearly to mind.

The progressive development of the horse family from the little, four-toed, generalized, ancestral type to the highly

* W. D. Matthew, Climate and Evolution; Annals New York Acad. Sci., Vol. 24, pp. 171–318, 1915.

specialized horse, rhinoceros, and tapir of today is one of the stock illustrations of the evolutionist. The evolution of the horse is clearly in the line of special adaptation to a peculiar environment. The foot has been made more and more efficient for locomotion over a smooth, regular, and rather hard surface, although the changes directed toward that end have made it less capable of travelling over loose ground and of little use for striking or grasping or any other of the varied processes for which the feet of many-toed animals are used. The increased length in the lower leg and foot have increased the length of stride without decreasing its quickness. The reduction and disappearance of the side toes and the concentration of the step on the single central toe serve to increase the speed over smooth ground. These changes in the limbs and feet made it necessary for the grazing animal to have a longer head and neck so that the mouth was enabled to reach the ground. At the same time, the record shows a change in the teeth, which have progressed from short-crowned to long-crowned. Thus the animal has been enabled to subsist on the hard, comparatively innutritious grasses of the dry plains, which require much more thorough mastication than do the softer green foods of the swamps and forests. "All these changes in the evolution of the horse are adaptations to a life in a region of level, smooth, and open grassy plains such as are now its natural habitat. At first the race was better fitted for a forest life, but it has become more and more completely adapted to live and compete with its enemies or rivals under the conditions which prevail in the high, dry plains of the interior of the great continents."*

So complete is the array of fossil specimens which show the various steps in this particular progressive development and so striking is the evidence that successively more equine animals lived in successively more recent time, that there is a strong tendency to interpret the history of the horse in terms of a certain kind of orthogenesis. The interpretation of some is represented by the frivolous little verse which finds its place in every paleontologist's anthology:

"Little Eohippus was no bigger than a fox,
And on four toes he scampered over Tertiary rocks.
'But,' said little Eohippus, 'I am going to be a horse,
And on my middle fingernails to run my earthly course.' "

* W. D. Matthew, Evolution of the Horse; American Museum, Nat. Hist., Guide Leaflet No. 36, p. 29, 1913.

Recalling the progressive development of many organic phyla, which seem to have moved directly toward a modern type, it is very easy for us to assume that the earlier members of the phylum were possessed of impulses directing them toward the attainment of a definite though distant goal.

As a matter of fact, of course, little Eohippus had no information concerning the characteristics of the noble steed which was to be his Pleistocene descendant. His highest ambitions were presumably to escape from the stealthy approach of an ancestral feline and secure for himself safe pastures on the western prairies. To understand the straightforward progress of the odd-toed, hoofed mammals, culminating in the modern horse, one must know the changing environment which accompanied the organic modifications. During the Age of Mammals, that portion of North America which we call today the Great Plains was undergoing a radical alteration. In early Tertiary time that region was low and moist, with many swamps and widespread forests. Apparently the cordilleran barrier between it and the moisture-laden winds of the Pacific was much lower than it is today. The physical record during Tertiary time is marked by a progressive desiccation and cooling of that area. This may have been in large part a response to the building of mountain barriers at the west, although it was undoubtedly due in considerable degree to changes in the earth's atmosphere which were bringing about a more pronounced zonal distribution of temperature. Whatever may have been the causes, it is clear that the evolution of the horse family paralleled an environmental change from forested lowlands to grassy prairies and treeless savannas. This seems to have been the directing influence. Each improvement of the ancestral horses in strength and efficiency of limb, in perfection of hoof, and in effectiveness of grinding teeth, seems to have been a response to demands made by the changing environment. The four-toed, and many of the three-toed, horses were forest dwellers accustomed to browsing rather than grazing, living on the soft, springy forest mold rather than the hard, unyielding turf of the prairies. The gradual diminution of the area of forests and the expansion of the prairies not only gave the opportunity but directed and impelled the achievement of the modern type of horse. Orthogenesis seems to be a response to progressive changes in environment rather than to definite ambitions with which a creature may be endowed.

GEOLOGIC FACTORS IN THE EVOLUTION OF MAN.

Although the main outlines of the story of man's origin through modification from an arboreal anthropoid ancestor are well known, many of the details of interest in this connection await discovery. Many students of this problem have inferred that south-central Asia was the region in which this development took place, but the inference is based as much on lack of knowledge as upon deductions from known facts. One must confess that Hrdlicka's contention that east-central Europe may have been the birthplace of mankind is well within the bounds of possibility. Regardless of our lack of knowledge concerning the locality, there is no doubt but that the ancestry of man is traceable through a strain of anthropoids which gradually changed their habits from those associated with life in trees to those made necessary by life on the ground. Barrell* has sketched an interesting picture of environmental changes in south-central Asia which he believes directed that modification of the "ape-man." Gradual desiccation and increasing cold are supposed to have caused a progressive dwindling of the forest areas north of the Himalaya Mountains. The treeless steppes of the northland expanded southward, and encroached more and more upon the wooded regions. Retreat toward the south was supposedly cut off by the new-formed barrier of the impassible mountain range, and necessity forced upon the arboreal anthropoids their modification to terrestrial life. It is fairly well established that the record of man's ancestry must have included some such modifications of habits and body structures, and these are much more likely to have been imposed upon the creatures by the external compulsion of environmental changes than to have been a response to ambitions innate within the anthropoid breast.

Every section of human history bears the unmistakable stamp of the geographic environment in which man progressed from primitive barbarism to the complex civilization of today. Geologic factors are the warp without which the tapestry of human progress could never have been woven. A single illustration will serve to suggest the close relationship between man and his environment. Miss Semple has called attention

* J. Barrell, Probable Relations of Climatic Change to the Origin of the Tertiary Ape-man, Scientific Monthly, Vol. 4, pp. 16–26, 1917.

to the intimate relations which exist between marine highways and the later stages of human culture. "The progress of history has been attended by an advance from smaller to larger marine areas, with a constant increase in those manifold relations between peoples and lands which the water is able to establish. Every great epoch of history has had its own sea, and every succeeding epoch has enlarged its maritime field. The Greek had the Aegean, the Roman the whole Mediterranean, to which the Middle Ages made an addition in the North Sea and Baltic. The modern period has had the Atlantic, and the twentieth century is now entering upon the final epoch of the World Ocean."*

The Caucasian race, reaching the shores of the inclosed or marginal seas which form the eastern Mediterranean, found there the nursery in which were taken the first feeble steps toward the conquest of the water. Success in that limited environment was followed by the opportunity to pass into the kindergarten of the open Mediterranean. With sharpened wits and strong hearts resulting from the lessons learned in that kindergarten, the white races were ready a little later to embark along the shores of the eastern Atlantic, and in the training school afforded by its embayments, coastwise navigation was perfected. Ere long, intrepid navigators matriculated in the college of the open Atlantic; and today their successors pursue post-graduate courses in the University of the World Ocean. Again, the story of life development is phrased in terms of capable individuals presented with opportunities inherent in particular environments. Had the outlines of all the continents been like those of Africa, one can but wonder if giant ocean liners would have been a product of the twentieth century or whether they must have awaited some far distant future time.

Any broad survey of the strain of life development leading to man as we know him today can not fail but impress us with the unique succession of felicitous events which in the last analysis are dependent upon the internal conditions and external relations of the earth itself. Progress from simple to complex, from lowly organisms to higher types, from primitive conditions to "better things," is by no means a necessary consequence of

* E. C. Semple, Influences of Geographic Environment, New York, 1911, p. 311.

life. The ceaseless urge within the living creature appears to be only an impetus making for change. Variation may be in any direction, for better or for worse. Environment and environmental changes seem to be the directive influences. It is hardly to be expected that another planet, even among the myriad planets which may pertain to the stellar galaxy, should have had a geologic history sufficiently similar to that of our earth to have developed life along similar channels. Although there is no apparent reason for assuming that life as we know it represents the only possible manifestation of the great mysterious vital forces inherent in the spiritual universe, here is a strong argument that man is actually unique both in time and space. The law of probabilities almost excludes the possibility that anywhere else or at any other time vital energy has manifested itself in protoplasm and that protoplasm has been led through the long chain of upward progress to a creature which would be even an approximate duplicate of mankind.

If geologic factors have thus directed the history of life development and thus in a very real sense are responsible for the coming of mankind, there is no escape from the conclusion that the future history of man will likewise be under the sway of environmental factors. The key supplied by knowledge of the past is the only key available with which to unlock the door of the future. Man, a product of environment, may boast about the success with which he has subdued the earth, but the quiet power of the constantly operative geologic factors continues to define the limits within which his future activities must be set. The geologist has reason to be very optimistic concerning the possible span of the future existence of the earth as an abode for life. "While there is to be, with little doubt, an end of the earth as a planet, and while perhaps previous to that end conditions inhospitable to life may be reached, the forecast of these contingencies places the event in the indeterminate future. The geologic analogies give fair ground for anticipating conditions congenial to life for millions and tens of millions of years to come."*

Man, so far as we can tell, is unique among all animals in the possession of a definite moral purpose, a purpose to utilize to the fullest his potential ability for the "higher good." That

* T. C. Chamberlin, A Geologic Forecast of the Future Opportunities of Our Race; Science, Vol. 30, pp. 937-949, 1909.

higher good in its ultimate materialistic aspect means simply the continued occupation of the earth by humankind for as long a period of time as possible. With such thoughts in mind it is obviously well worth while to inquire into the place in which we find ourselves in the year 1924 when viewed in the long perspective of the whole existence of man as an animal species set in a peculiar if not unique geographic environment.

Homo sapiens is still a youthful species. His present span of life is measurable by some such figure as forty thousand years. The total span of existence of the individual species of air-breathing vertebrates has probably averaged three or four hundred thousand years. Our knowledge of the antiquity of many existing species of vertebrates indicates that among the present population of the lands, man is distinctly a newcomer. He has not yet lost the plasticity and virility of youth. He is still in the adolescence of the species and has not yet settled down into the conservatism and inflexibility of racial maturity.

The youthful species has been passing through a stage of provincial development and is even today embarking upon a more cosmopolitan career. The spread of mankind over the habitable globe has placed different individuals in diverse and isolated environments. Each continent has developed its own racial varieties. Each geographic region has witnessed the evolution of racial subdivisions having each its own distinctive characteristics. The differentiation of mankind into scores of ethnic strains has doubtless been directed in no unmistakable degree by the diversity of environmental conditions which man has found in the progressive peopling of the lands. But the last three centuries have witnessed the breaking down of barriers. Mountain and sea, forest and desert no longer serve to separate human provinces. Distance has been annihilated; barriers have been surmounted; isolation is today well nigh impossible.

Man has utilized his best ingenuity and greatest strength in an attempt to mold his geographic environment toward a uniform type. Deserts are irrigated; swamps are drained; forests are cut down; scattered clumps of trees are carefully planted and nurtured on wind-swept savannas. As a geographical agent, man works consciously toward uniformity. The world is fast becoming a neighborhood. In consequence, differentiation is waning almost or quite to disappearance.

Racial fusion or assimilation is now taking the lead. The provincial types are mingling and modifying into the cosmopolitan. For man, as for every other creature, that transition from provincial to cosmopolitan types is a time of appraisement and testing. The products of the varied provinces are now balanced against each other. The least fit must inevitably be submerged, while the more efficient and better qualified contribute largely to the final product.

But that does not mean that the most selfish, most powerful, most numerous, or even the most clever of the varied human types, from which selection is even now being made, will be the type for cosmopolitan humankind. The strain that leads to man has been clearly characterized by an increasing breadth and depth and strength of the cooperative spirit. Back at the dawn of human history, when our anthropoid forefathers maintained a most precarious existence among carnivorous mammals, to whose depredations they were exposed more and more frequently as the comparatively safe haven of the forests disappeared from the expanding prairies, the necessity of cooperation for attack and for defense was ingrained in every human survivor. The social history of man is marked by constant increase in the unit within which cooperation is workable. Family life has been submerged within that of the clan; clans were associated into tribes; tribes, into nations; nations, into alliances and leagues. Note how the geologic factors impose upon the future progress of mankind far greater and more intelligent cooperation than has yet been attempted.

Human development has thus far been marked by expansional evolution. There have always been vacant lands available for settlement, when the constant press of growing population made necessary the expansion of a community by migration or colonization. Only in times of war or in such communities as the densely populated valleys of India or China has mankind in large units ever faced the absolute necessity of conserving with utmost frugality all available food supplies. It is perfectly possible today, as it has always been in the past, for mankind to secure an abundance of food for every member of the human family. All that is required is a reasonable amount of industry and an intelligent distribution of products. But this period of expansional evolution cannot continue many centuries longer. For man, as for Paleozoic invertebrates, the

tide must turn. Expansional evolution will give way to restrictional development. Exactly how many billion human souls may find sustenance upon our earth no one can accurately estimate, but that there is a limit to the possibilities of the earth as an abode for human beings, no careful thinker who does not blink at facts can possibly deny. The limit may be as low as four billions, or as many as ten, but somewhere there is a deadline.

Far back at the very beginning of life development upon our earth, man's remote Protozoan ancestor sacrificed the ability to utilize the energy of the sunlight and make food for itself from inorganic compounds. That sacrifice bore rich fruit in the deployment and perfecting of animals of all sorts. Not the least of its consequences is just now being impressed upon mankind in the compulsion toward cooperation. Dependent upon other organisms, in the last analysis, plants, for sustenance, the future generations must conserve all available food supplies and develop to the utmost a thoroughly reliable and adequate network of transportation facilities. Mutual interdependence will become more and more apparent as the total population approaches more and more closely its ultimate limits.

How many generations will elapse before the present sixteen hundred million people on the earth have multiplied until the population reaches its absolute maximum, no one can tell. Decreasing death rates and decreasing birth rates can scarcely be balanced accurately one against another. The conquest of the tropics is well begun, but the conquest of polar lands has only recently been suggested. Very possibly, amelioration of climate with increasing chronologic distance from the last ice age may appreciably expand the areas available to serve as man's domain. Even within a few hundred years, considerable changes in the earth's atmosphere, due to man's activity in this industrial age, may react favorably by causing further diminution of arctic and antarctic ice fields. Turning from the long perspective of the many tens of thousands of years since the Cro-Magnon race of *Homo sapiens* lived in southern Europe, the few centuries which remain before the earth will have been completely populated by mankind seem to the geologist extremely short.

From the geologic point of view, therefore, the next great crisis in life development is even now imminent, relentlessly

forced upon us by geologic factors. The success with which living creatures have weathered every such crisis in the past is fair ground for optimism that this crisis of tomorrow will likewise be successfully negotiated. As in the past, so in the future, success comes because a minority respond to the challenge flung by environmental factors. The pioneers of progress have invariably been a hardy, risk-taking group, endowed with specific virtues which gradually make their way against an overburden of opposition.

Survival values in the past have generally been measured in terms of physical adaptation; survival values in this coming crisis will apparently be psychical rather than physical. Man is unique among animals in several ways, not the least important of which is the fact that he has specialized not along the line of adaptation to any one environment, but along the line of adaptability to all environments. His physical adaptability almost rules out of consideration the physical factors as determiners of survival value. Apparently, therefore, the qualities which will determine man's ability to negotiate successfully this next great crisis in life development will be psychical—mental, moral, and spiritual. Willingness to cooperate with his fellows, coupled with intelligence in devising cooperative ways and means, will be the measure of man's fitness individually and collectively to survive.

CONCLUSION.

The geologist, fresh from his survey of geologic factors in life development, has every reason to take an optimistic outlook for the future of mankind. As the twig is bent, so the tree is inclined. Geologic factors in the past have directed life onward and upward to its present high plane. A physical organism has been perfected to such a degree that it possesses a knowledge of moral law, a sense of rightness, a confidence that its reasoning mind finds response in a rational universe, and a hope that its spiritual aspirations will find increasing answer in a spiritual universe. Intelligent enough to read the record of the past and face the problems of the present, it is inconceivable that man should fail as he attempts to develop within himself a spirit of cooperative endeavor strong enough and intelligent enough to insure his success in the critical moments of the future.

PRINCIPLES OF PLANT TAXONOMY. I.*

JOHN H. SCHAFFNER
Department of Botany, Ohio State University

In 1905, the writer began publishing a series of papers on the phyletic classification of plants, which gave a general arrangement of the entire plant kingdom and also a discussion, in an elementary way, of the evolutionary facts on which a true classification must ultimately rest. These papers appeared in The Ohio Naturalist and its continuation as The Ohio Journal of Science. No. I appeared in Vol. V, 1905; Nos. II and III in Vol. VI, 1905–6; Nos. IV and V in Vol. IX, 1909; Nos. VI and VII in Vols. XI and XII, respectively, 1911; Nos. VIII, IX, X and XI, in Vols. XIII and XIV, 1913; and No. XII, after a long hiatus, in Vol. XXII, 1922.

It is now the intention to publish a new series with special emphasis on the facts which appear to be of importance in determining a correct, evolutionary arrangement and phylogenetic classification. Some of the material given in the previous papers will not be repeated, but some of it will be considered and restated in the light of a more complete knowledge of plants, acquired by the writer through his own efforts and those of other investigators. The subjects treated will be taken up more or less at random, sometimes presenting a general aspect of the subject and sometimes a special case considered in detail.

THE SEVEN FUNDAMENTAL DIVISIONS OR SUBKINGDOMS.

In order to obtain a correct background for any scheme of classification, it is of the grestest importance to discover what have been the main movements and evolutionary advancements that have taken place in passing from the lowest to the highest types. Without reference to any notion of phyletic relationship, what is the general nature of the various types of higher and higher plants as one takes a general view of the whole plant kingdom? Such a view presents seven definitely marked stages

* Papers from the Department of Botany, the Ohio State University, No. 147.

or subdivisions, no more and no less; and each higher division is characterized by the acquisition of fundamentally new properties and activities, which result in new complexities in the life cycle, physiological processes, and structures. At each of the six transition stages some fundamental property or relation is added which is retained, after that, throughout all succeeding stages and is very rarely lost in individual cases. The emphasis will be placed on fundamental processes and physiological relations rather than on structures, as has usually been done, for it has become plain that the structures developed in any individual result from the presence of hereditary factors through the physiological activities of the cells in the given environment. In placing the emphasis on fundamental properties and functions, our classification will appear in a clearer light as simply a systematizing of the evolutionary progressions. and a more or less correct chronological arrangement of the more and more complex heredities that result in new activities, interrelations, and structures of cells and organs as one passes up the ladder of organic forms. There are, of course, morphological characteristics which delimit the subkingdoms very distinctly except the two lowest, which are separated on purely physiological grounds, since the lowest sexual forms show no dimorphism even in the gametes. But as stated above, the morphological characters are in the end merely the result of activities dependent on the presence of a given heredity in a given environment, and by emphasizing morphological features in the segregation of the great progressive divisions the attention is diverted from the main point of importance and interest. It is also possible to define the seven subkingdoms entirely in terms of their life cycles. Each group has one or more characteristic life cycles; that will clearly segregate it from all others except in the case of low forms without secondary sexual characters that have lost their sex.

The lowest plants are then apparently without sexuality. The organization of their protoplasts is apparently such that no sexual states arise under any known conditions. These nonsexual plants include unicellular and colonial forms and multicellular forms with cell differentiation. Some might object to the recognition of these plants as a distinct subkingdom since abundant unicellular forms occur which have well-developed sexual states, but since the upward evolution of the

plant kingdom is so intimately associated with changes in the relation of the sexual state to the life cycle, it is necessary from theoretical grounds to lay emphasis on the fact that the first type of living things that appeared on the earth was apparently nonsexual and has so remained. These primitive, nonsexual plants constitute the subkingdom PROTOPHYTA.

In general, plants proceed from the unicellular to the multicellular condition, both in the ontogeny and in the phylogeny, but the transition is so gradual and involves so little change in the functional nature of the organism that it is impossible to separate the unicellular from the multicellular. In fact it is much more difficult to segregate the strictly unicellular from the strictly multicellular than to separate those with sexual states from the non-sexual. The difficulty arises because sexual organisms may fall back into such a condition that no sexual state ever develops.

In the higher forms which have lost their normal sexuality, partial or secondary sexual states arise, but in one way or another the perfect, primary sexual state is not attained and the species continues either parthenogenetically or apogamously. In the lower, unicellular and colonial species it is often difficult or impossible to form a convincing judgment as to whether the organism in question was derived from a previous sexual condition or whether it represents a direct derivative from the original nonsexual state. Such cases must be decided by a study of the complexity of the cell in general and the nucleus, and by a comparison with the nearest relatives. Usually there will be less uncertainty than there is in separating lower "plants" from lower "animals." The other five transitions offer no such difficulties. In fact with an ordinary knowledge of the morphology and life history, every species can be placed with absolute certainty. There are attraction stages in some lower organisms which in physical nature may be somewhat akin to sexuality which, nevertheless, are to be regarded as distinct phenomena not related to sexual states, namely the aggregations, fusions, or associations of cells at certain periods, as manifested in Myxobacteriales, Myxophyta, and Hydrodictyales.

In general, plants proceed from the uncellular through the colonial state to the multicellular condition, with little change in the functional nature of the organism. However, the

change from unicellular to multicellular frequently also involves a change from nonsexual to sexual, although these two evolutionary progressions are apparently due to fundamentally distinct causes.

The second subkingdom is named NEMATOPHYTA because of the prevalence of the filamentous condition in most of its classes, and because in the two succeeding subkingdoms the gametophyte usually passes through a protonema stage in its embryogeny. In this subkingdom there are three main types of life cycle: first, a simple sexual cycle with a haploid individual; second, a simple sexual cycle with a diploid individual; and third, an alternation of generations cycle with a haploid individual alternating with a diploid individual, the diploid individual being independent of the haploid individual, although in some cases a diploid, spore producing parasitic phase is present at first as in some red algæ. This alternation cycle is therefore quite distinct from the one which appears in the next higher subkingdom and which remains fundamentally unchanged to the highest plants. Each of the three life cycles of the Nematophyta may be modified in one way or another in details, the most extreme, perhaps, being the modification of the alternation cycle in such higher fungi as the rusts, where the diploid generation consists of cells with pairs of haploid nuclei rather than of cells with diploid sets of chromosomes in conjugated nuclei. Such a condition could arise if the conjugating nuclei lost, for the time being, their primary sexual states or property of attraction before coming in contact and developed it again at the end of the diploid generation stage. In contrast to the diversity of life cycles in the Nematophyta, each of the subsequent subkingdoms has but one general type of life cycle and, as stated above, all are mere modifications of one fundamental type.

The second transition in the plant series is that which leads up to the BRYOPHYTA. This is by far the greatest break or hiatus in the plant kingdom from a morphological point of view, there being no possible direct connection until one passes down to the very simple green algæ of the confervoid type. The higher green algæ have not only a different life cycle, but entirely different sexual organs. The gametangia of the Bryophytes come close in structure to those of certain brown algæ, but there is no possibility of a direct relation with this

group. So a series of hypothetical forms must be postulated for the ancestry of the liverworts and mosses. The transition to the Bryophytes marks the change from plants adapted to an aquatic habitat to those adapted to live and thrive in aerial conditions. Many Thallophytes are adapted to endure aerial conditions but usually they can only grow well during very wet periods or in very damp places, except some parasites which are, of course, supplied with moisture by their hosts. The lower types of Bryophytes are not entirely weaned from the aquatic habit, but the higher species usually show a greater and greater modification toward dry-land conditions, which finally becomes the goal of the evolutionary process. All along the line, however, there may be, here and there, a return to a secondary aquatic life. A second characteristic of the third subkingdom is the new type of antithetic alternation of generations with a permanently parasitic sporophyte. This new life cycle with its twelve fundamental, antithetic stages is retained, but evolved into a more complicated succession of intermediate stages, step by step, to the highest plants. Its presence or absence becomes a definite division line for the entire plant kingdom into Thallophytes and Meta-thallophytes. The archegonium is a new type of ovary which is barely hinted at in the Nematophyta, and the development of numerous sporocytes in a special tissue is also characteristic.

The third subkingdom, or BRYOPHYTA, may, therefore, be defined as those plants which have an antithetic alternation of generations and a permanently parasitic diploid sporophyte. The sporophyte is always homosporous. One of the most interesting developments in this subkingdom is the remarkable evolutionary advancement of the sporophyte, which passes from the condition of a simple sporangium or sack of nonsexual spores to a highly specialized individual containing a foot, stalk with a conducting strand of cells, hypophysis with true stomata and photosynthetic tissue, and a highly specialized sporangium; and in one group an intermediate growing zone, which is the first indication of indeterminate growth. Parasitism in this case has certainly not led to degeneration, but has led the way toward a condition of highly organized independent existence. By no possible stretch of the imagination could this series be considered as a reverse evolution.

The third transition, which is also a prominent hiatus, leading to the fourth subkingdom, is the consummation of the development carried forward in the evolution of the Bryophytes, namely, the change from a permanently parasitic sporophyte to a sporophyte with two distinct stages or phases in its life-history, first a juvenile parasitic stage and second a mature independent stage in which roots, true vascular tissue, highly organized leaves, and indeterminate buds are developed. The sporophyte with its indeterminate growth shows an enormous advance over the determinate sporophyte of the Bryophytes. Its early parasitic condition can properly be interpreted as being derived from a completely parasitic condition similar to that of the Bryophytes. The fourth subkingdom, or PTERIDOPHYTA HOMOSPORÆ, may, therefore, be defined as those plants with a typical alternation of generations in which the sporophyte has two distinct stages, a parasitic stage and an independent stage, and which is homosporous, the sexual state being normally determined in some stage of the development of the gametophyte. The life cycle of the Homosporous Pteridophytes, therefore, is essentially the same as in the Bryophytes, except in the peculiarity of the sporophyte having two distinct stages of existence, although the morphology of the sporophyte shows an enormous advance over the previous condition. There is no apparent ancestor among the Bryophytes, although the Anthocerotæ suggest a possible distant relationship to the hypothetical ancestors of the Pteridophytes. All plants above the Bryophytes have sporophytes with the two stages, but in some cases, of course, the second stage may be a parasite on a foreign host.

The fourth transition leading up to the fifth subkingdom is again, like the first transition, especially concerned with the sexual state. The determination of the sexual state is transferred back from the gametophyte or the spores from which the gametophyte originates to the tissues of the sporophyte generation, and as in the original evolution of sexuality, so here also, the transition appears to have occurred in a number of independent groups. Although the gap between the living Heterosporous Pteridophytes on the one hand and the Homosporous Pteridophytes on the other is small, it represents one of the most important and profound changes in the whole evolutionary progression. Below, sex is determined in haploid individuals

and above in diploid individuals. It does not seem possible that anything like a seed plant could have evolved without this preliminary step. All plants above this transition are heterosporous and always show some sexual dimorphism in the sporophyte, although in the lowest this dimorphism does not extend beyond the tissues of the sporangium and its stalk. In the extreme cases sexuality is determined in the zygote and thus the entire individual may show secondary sexual dimorphism.

Along with the transfer of the time of sex determination to the sporophyte goes a great reduction in the size and complexity of the gametophyte, which must now, of course, under normal conditions always be unisexual. This extreme reduction naturally leads to the next great transition, the development of seed plants. The PTERIDOPHYTA HETEROSPORÆ may be defined as those seedless plants in which the sexual state is determined in the tissues of the sporophyte and in which the gametophyte is greatly reduced, but is not entirely parasitic on the sporophyte, although there may be a beginning of parasitism in the juvenile stage. The life cycle becomes much more complex since there are now two kinds of sporangia, two kinds of sporocytes, and two kinds of nonsexual spores.

The change from the Heterosporous Pteridophytes to the next higher subkingdom, the GYMNOSPERMÆ, is from independent gametophytes to completely parasitic gametophytes, the spores not being shed. The female gametophyte is permanently parasitic in the megasporangium and the male gametophyte or pollen grain is at first parasitic in the microsporangium and later, on the megasporangium or ovule by means of the pollen-tube. This parasitic pollen-tube is a structure characteristic of all seed plants and along with numerous other peculiarities indicates their high position. So seed plants may be defined as those plants which have a male gametophyte with two distinct parasitic stages. Another fundamental change from the condition in the Homosporous and Heterosporous Pteridophytes is the intercallation of a resting period between the parasitic and independent stages of the sporophyte. From the liverworts on up there are, therefore, three prominent steps in the progressive evolution of the sporophyte. In the Bryophyta, the sporophyte is continuously parasitic and determinate in growth. In the Pteridophyta, the sporophyte

has an embryonic parasitic stage followed, through a gradual change, by an independent stage with an indefinite period of growth. In the Spermatophyta, a profound resting period, with a subsequent re-awakening or sprouting, is almost universally developed between the parasitic embryonic stage and the later independent stage of growth.

The typical seed plant has been completely weaned from a free water habit by taking the gametophyte from the ground and by conducting the sperms to the ovaries by means of the pollen tube. The Gymnospermæ are, therefore, the higher plants with parasitic gametophytes in which the male gametophyte falls directly into the micropyle of the ovule during pollination and thus develops a short pollen-tube, since the carpel is open and without a stigma.

It may be noted, in passing, that with the development of the seed and the resting period of the sporophyte embryo, the young sporophyte is largely taken out of the struggle for existence. It is an interesting fact that the highest plants, like the highest animals, have evolved this special care for the young of the next generation. And it is still more wonderful to contemplate all the complex changes in structures and functions that had to take place simultaneously or in close succession, in the evolution of these plants, if the complex arrangement was to work at all.

The sixth transition leading to the final or seventh subkingdom, the ANGIOSPERMÆ, is marked by the closing up of the carpellate leaf and the development of a stigma. Pollination is, therefore, no longer on the micropyle of the ovule but far removed and the pollen-tube is correspondingly long, having an extensive development before reaching the ovule. The second parasitic state of the male gametophyte has become highly perfected. It is interesting to note that among the ferns some groups also chose their leaflets over the sporangia. Since living seed plants were apparently all derived from the ferns it is only natural that there should be both open and closed sporophylls. The gametophytes of Angiosperms hold in general the same relations as those of the Gymnosperms, but are reduced to an extreme degree. A new development also is the process of triple fusion from which a new triploid tissue is produced beside the embryo sporophyte. This endosperm or xeniophyte is not present in the Gymnosperms, although there is occasion-

ally a fusion of the ventral canal cell with the second sperm of the male gametophyte. In a few Angiosperms more than three cells may be concerned in the formation of the initial cell of the xeniophyte. In the Angiosperms, therefore, normally five conjugating cells are in evidence at the fertilization period rather than two, as in other plants. In the Angiosperms which have primarily bisporangiate flowers with the stamens below, there is very commonly a showy perianth produced through the sterilization of the lower stamens. There is also some slight sterilization of basal sporphylls in some of the Gymnosperms, but this is never very prominent.

The transition to the Angiospermæ represents an enormous gap. There is apparently nothing so far known to indicate the line of ascent from their probable ancestors, the eusporangiate ferns. The Angiospermæ do not have any direct relation to any of the Gymnospermæ unless perhaps the Pteridospermæ. But the Pteridospermæ seem rather to be in the direct line leading up to the Cycads, Cordaites and Ginkgoes.

These then are the fundamental steps in the ladder of ascent in the plant kingdom. There are seven stages, no more and no less; for although in each of the seven subkingdoms there is a progressive advancement, this does not at any point involve a fundamental departure from established structures and functions taken by all the members, but rather a gradual advancement taken in one or more lines in the subkingdom and not marking a distinct or abrupt transition from lower to higher.

All of the higher plants are flowering plants, namely, they have their sporophylls developed on determinate axes, but the change from flowerless plants with indeterminate sporophyll-bearing axes to flowering plants takes place at entirely different levels in different groups. In lycopods and horsetails the strobilus is attained in the homosporous state. Apparently none of the ferns, either eusporangiate or leptosporangiate, and none of the quillworts evolved determinate sporophyll axes, and in the Cycadophyta the seed habit was well advanced before flowers appear. There are still two living genera of seed plants which show a flowerless condition and there is no plausable reason for supposing that they were ever any different in this respect.

In Ginkgo, neither stamens nor carpels are produced on determinate axes, although some interpret the single stamen and the single carpel as highly reduced strobili. But the latter view has little weight, for practically all the evidence points unmistakably in the other direction. In Cycas the determinate axis is a sex limited character, being developed only in plants in the male state, the carpels being produced in rosettes on the indeterminate main axis of the carpellate plant.

In the broadest sense, therefore, the presence and absence of the flower does not form a basis for grouping the higher plants into primary divisions, although after it once gets well started along the evolutionary pathway, it becomes an organ of decided progressive and segregative tendencies. It might be added that fundamentally the higher types of flowers do not differ from the lower, although as the term is popularly applied it might be inferred that Angiosperms have "flowers" and other plants do not. But there is no basis for such a notion unless the flower is defined in purely arbitrary terms.

To summarize, the evolution of the seven fundamental stages is as follows:

1. The lowest plants are non-sexual.

2. The change to the second stage is the evolution of the cell to a condition that sexual states appear from time to time, giving rise to cell conjugations and three general types of life cycles.

3. The second transition is to plants with a typical, antithetic alternation of generations life cycle with twelve fundamental stages, and with a permanently parasitic, determinate, homosporous sporophyte.

4. The third transition is to plants with a similar life cycle but having a homosporous sporophyte of indeterminate growth with two distinct stages of existence, a parasitic juvenile stage followed by an independent mature stage with roots, leaves and vascular tissue.

5. The fourth transition is to plants which have their sexual states determined in the sporophyte which thus develops, in distinct dimorphic sporangia, male producing microspores and female producing megaspores. There is also a decided tendency toward extreme reduction of the gametophyte.

6. The fifth very pronounced transition is to plants which have parasitic gametophytes, the male gametophyte having a two-phased parasitic life, the first stage in the microsporangium and the second in the megasporangium by means of the pollen tube. The sporophyte has a resting stage intercallated between its parasitic and independent phases. In the subkingdom immediately above the transition the transfer of the pollen (pollination) is directly to the micropyle of the ovule and there is no xeniophyte or true endosperm developed.

7. The sixth transition is to the highest plants with a specially developed structure, the stigma, for the reception of the pollen or male gametophyte, because of the closing up of the carpel. In consequences of this a long pollentube is developed which finally grows into the ovule. The gametophytes show the most extrement reduction and there are typically five cells concerned in conjugations during the fertilization period, a male and a female cell uniting, as in the plants below this stage, to form the initial cell of the diploid sporophyte, and a male cell and normally two cells from the female gametophyte uniting to form the initial cell of the xeniophyte or triploid endosperm. Probably universally, by a sterilization of stamens, a perianth is produced, which may be lost again through reduction.

The seven subkingdoms which form the foundation on which all plant classification must be constructed are, therefore, the following.

VII. Angiospermæ.
VI. Gymnospermæ.
V. Pteridophyta Heterosporæ.
IV. Pteridophyta Homosporæ.
III. Bryophyta.
II. Nematophyta.
I. Protophyta.

The Class.

As shown in the discussion above, the seven subkingdoms or divisions do not represent natural or phyletic groups. In only two cases is there any direct connection between members of a lower subkingdom and those immediately above and both these transitions are in relation to the determination of sexual

states. It is because of their sharp demarkation from each other that the subkingdoms become the basis for the segregation of the fundamental major plant group units, the classes. A class is the largest, definitely determined, monophyletic group in a subkingdom. A class may be defined, therefore, as: *The largest group of plants in a subkingdom the members of which show an evident relationship to one another as compared with the members of some other group or groups in the same subkingdom.* The emphasis is to be placed on the word "evident," which involves an exercise of judgment by the classifier. Such an exercise of judgment is not required in establishing the seven subkingdoms.

In determining how great or how small a group shall constitute a "class," practical considerations should also have weight. Convenience in delimitation and definition of the group, its practical use in applied science, the advantage in not having too great a number of such units, so that they can be easily retained in the memory, and other similar considerations should be the main criteria in determining the approximate number to be established. The problem is not very different from the one in which a decision is made as to how many large or main branches a given tree with a complex branching system may have. By exercising his own judgment and adopting the work of others the writer has recognized about fifty classes. Some of these classes fall naturally into two or more subclasses and some are so large that a division into subordinate groups, higher than the order, becomes necessary for convenient treatment. These subclasses should also be limited in number for the same reasons as those given for the class. By a reasonable segregation method, the number of classes and subclasses combined falls well below the hundred mark.

With the establishment of the class as the fundamental unit which can be defined quite definitely as to its limits, the systematist has a group which becomes the basis for classification in its broadest aspects. Classes can be compared as to probable relationships and combined into the main branches or *phyla* and *subphyla* on the one hand, and on the other they can be divided into subordinate divisions, the orders.

The Species.

Just as the classes are the units in thinking and treating of plants in their general aspects and in establishing higher groups by combination or lower groups by division, so the species are the units for dealing with plants in their severalty in the science of botany in general and in all the practical relations of life. The species name, whether scientific or common, serves as a means of general communication. The species then must apply to a unit of classification which is both scientific and practical. Too great a refinement of segregation leads to an impossible system for the practical man as well as the botanist who is not especially acquainted with the given group, both because of the impossibility of definite identification and the evident impossibility of keeping a multitude of names in mind based on trivial and wholly unimportant differences. It is not the desire to attempt a definition of species here but simply to make a few practical observations. It soon becomes evident to any one dealing with diverse groups of plants that the concept for specific limits must be different for different groups, not only because of differences in the groups of organisms themselves, but also because of the special practical relations which the members of various groups sustain to mankind. In a general way, the Linnean species make suitable phylogenetic units and the term "species" should be retained for them. A serious attempt should be made to define species in such a way that the term can not be continually shifted to smaller and smaller divisions as is now being done very prominently, especially in some genera. The recognition of smaller units than the species is of great importance in certain lines of study, but definite provision should be made for lower categories within the species to any extent that may be desirable while leaving the larger Linnean units intact.

Many attempts have been made to define a species, but with only partial success. In nonsexual groups, evidently, the species can only be determined and defined by the degrees of morphological and physiological differences, but in the sexual plants, where interbreeding takes place, the species must be established on a different basis. Certainly all the forms that interbreed freely with fertile offspring are to be regarded as belonging to a single species. On the other hand, inability to

cross breed is not to be made a basis arbitrarily for species segregation, since we know that there is self sterility of the individual in many groups and often two very closely related varieties may be sterile toward each other.

In classification, the species are to be used as units of comparison in determining the next higher group, the genus. On the other hand, as intimated above, the species may be divided into smaller categories to the extreme degree, ending in the segregation of unit characters. In dividing species into smaller groups, experimental methods are to be employed; in sexual organisms for determining hereditary units, and also for determining fluctuations of ecological variations in both the sexual and the nonsexual. The study of the species resolves itself into genetic analysis on the one hand, and ecological variation or fluctuation on the other. In any freely interbreeding group, the subdivisions of the species are practically all of the same value, but for convenience standard varieties may be established based on some character or set of characters of special practical value, as for instance the consistency of the endosperm which is commonly used for segregating the main varieties of Indian corn, as pop corn, flint corn, sweet corn, etc. These endosperm characters are no more fundamental than various others that might be taken as for example pericarp colors, length of internodes, etc. But such classifications have less value from a practical standpoint. In the subdivision of economic species, therefore, the first consideration should be utility and there is no special reason why this principle should not be carried over to the non-economic species as well, wherever there is free interbreeding.

In taxonomy there are, therefore, two units of special importance, the class and the species. Both of these units must be constantly used in all studies of the evolution and classification of plants on the one hand, and in the practical application of plants in plant industry and the arts, on the other.

Since the species is considered and named in relation to the genus, the genus must also receive due consideration involving both the practical and theoretical sides. A system of names must be devised and established to insure at least a reasonable stability, otherwise the language of botany in so far as it concerns

specific names becomes burdensome and even ridiculous. It is remarkable that up to the present time there has not even been developed a system of generic types by which the names could become fairly well stabilized. It is to be hoped that this subject will now receive the serious attention it deserves from systematists.

DIMENSIONS OF THE CINCINNATI ANTICLINE.*

GEORGE D. HUBBARD
Department of Geology, Oberlin College

HISTORICAL.

The structure mentioned in our subject was recognized in 1838 by Locke,† who was in the employ of the Geological Survey of Ohio. He was making a survey of southwestern Ohio and after examining feeble local dips "in all possible directions," he observes that "when we examine the several formations on a large scale, the true dip becomes very evident; and as one formation sinks gradually below the surface, and another superior one presents itself, they give rise to those important changes in the face and products of the country." In correspondence with Owen, of the Indiana Geologic Survey, Locke also discovered that the strata lay similarly in Indiana, but that they dipped gently westward, while in Ohio they descended eastward. The dips thus recognized were so feeble that contact instrumental measurements could not disclose them, but through careful work with leveling instruments over considerable distances the actual dips were established.

Locke does not call it an anticline, but he clearly recognizes the structure, for he says, "on ascending the Ohio River eastward (from vicinity of Cincinnati) we meet with the blue limestone, cliff limestone, slate (shale), fine sandstone, conglomerate and coal, while descending the Ohio westwardly we meet with the same things in the same order."

In 1873 Newberry‡ discussed the structure and formations in Ohio and distinctly recognized and named the Cincinnati Arch. He says its axis is through Bethel, Ohio, and its breadth in Kentucky is 130 miles, but narrower in Ohio. He adds as confirmation that "outcrops of Corniferous (Devonian) limestone, which may be said to form its base on either side, are 150

* Presented before Sec. E, A. A. A. S., Cincinnati, O., Dec. 29, 1923. Published by permission of Dr. J. A. Bownocker, State Geologist, Geol. Surv. Ohio.

† Locke, Prof. John, Geol. Surv. Ohio. Sec. Ann. Rept. W. W. Mather, 1838, p. 206.

‡ Newberry, J. S., Geol. Surv. of Ohio. Vol. I, pp. 1–103.

miles apart in Kentucky and only 50 in northern Ohio.* He also observed that east dips were stronger than those to the west, but that all were very weak, mentioning 11–40 feet per mile. He also states that there are two folds in the crest of the main structure in northern Ohio.

Robt. R. Bell, of the Canadian Geologic Survey, has reported the geanticline as far north as Lambton, Ontario, at the southern end of Lake Huron. It is very low here and cannot be traced much, if at all, beyond this point, but it has here been a very productive source of fuel. Hall† recognized the Cincinnati Geanticline or Uplift, as it is variously called, and discussed its age and relation to Paleozoic seas, but as such matters do not fall within the scope of this paper, they will be all passed over.

In 1866 Gorby‡ devoted a dozen pages to a discussion of the Wabash Arch, which is the westward branch of the Cincinnati Anticline. This westward branch, says Gorby, possesses "absolute evidence of an upheaval extending from the northern part of Indiana near the Ohio line, northwesterly by Chicago to the regions of Lake Superior." (p. 240). He even follows a "learned paleontologist" in the suggestion that "this line or axis of upheaval is a projection of ancient disturbances, which originated in the volcanic regions of Lake Superior." (p. 229). There seems to be no reason, however, to consider the structure beyond Kankakee, Illinois, for it is well flattened out at the Illinois-Indiana line and seems to be lost near that place.

In 1893 Cubberly§ discussed the distribution of the Trenton limestone in Indiana by means of a map and a series of sections in various directions across the state. These sections and maps were based on many drill logs. The report shows the course of the Wabash Arch. It probably divides from the Cincinnati Arch a few miles south of Cincinnati, so that its axis is recognizable at Patriot, Indiana, and may be traced northward to Brookville, where it begins to divide again. Two folds or swells, one 6–8 miles west of Richmond, and the other 5–6 miles west of New Castle, are separated by a shallow sag and fuse again

* Geol. Surv. Ohio. Vol. I, 1873, p. 99.

† Hall, James, Pal. of N. Y. 1859. Vol. III.

‡ Gorby, S. S. Dept. of Geol. & Nat. Hist. of Ind. 1886. 15th Ann. Rept., pp. 228–41.

§ Cubberly, E. P. 18th Ann. Rept. Geol. Nat. Hist. of Ind., pp. 219–255.

into one toward Muncie and Anderson and beyond to Logansport. Near Rensselaer the arch again divides for a short distance as in northern Ohio.

In 1922 Malott* called attention to the trend of the axis in Indiana and to the relation of the arch to the strata and to topographic forms.

These two axes, one in Indiana, the other mainly in Ohio, if followed southward are found to unite just south of Cincinnati into a single broad swell or geanticline, which attains its maximum altitude as a structure in Jessamine County, Kentucky, in what is called the Jessamine Dome.

Toward the south the anticline can be traced easily across Kentucky and Tennessee into northern Alabama. The structure flattens out about 75 miles southwest of the Alabama-Tennessee line and passes under Cretaceous sediments. Becker† suggests that the Mesozoic and Tertiary strata of the coastal plain south and westward from this place show a broad low fold which can be traced across Mississippi and Louisiana. This of course is much later than the Cincinnati Anticline in as much as the latter was uplifted, arched and base leveled before these more recent beds were laid down. Hence it would probably be wiser not to consider such a structure as a part of the Paleozoic Cincinnati Anticline at all.

Summing up then we have a great Y-shaped structure whose south pointing stem is at least 300 miles long, whose eastern arm is of equal length between the fork and Lambton, Ontario, and whose western arm sweeps in a broad curve toward Kankakee, Illinois, with a length of 225 miles from the fork.

The anticline must be thought of as a structure and not as a form. While strata are everywhere in it arched into a grand, broad, low fold, the land along the crest is no higher than in other parts, and often not so high by a few hundreds of feet as the cuestas of flanking harder layers outcropping parallel with the axis.

---

* Malott, Clyde A. Ind. Geol. & Nat. Hist. Pt. 2. p. 127f.

† Becker. oral communication at Cincinnati meeting Sec. E. A. A. A. S. Dec. 29, 1923.

THE SECTIONS.

In order to carry forward this study, a series of structure sections have been drawn crossing the Anticline at selected places. Each section is essentially at right angles to the axis where drawn, and all are drawn on the same scale. In order that the arching may be visible, the horizontal and vertical scales hold such relation to each other that the vertical is exaggerated eight times. This makes the structure seem higher than it is, and portrays the dips much steeper on the flanks than they really are. We have, from its discovery, been told that it is a broad low arch, dome, fold, or anticline, but if one examines these sections and recalls that the vertical has an exaggeration of eight, he will be more than ever convinced of the value of the adjectives broad and low.

Since the relief of the land is so slight and generally more closely related to streams and valleys than to the structure of the anticline, the surface of the land is usually represented by a straight level line. A few valleys show and are so designated. The total relief over the whole area except for a few knobs in eastern Kentucky and others in central Indiana, probably does not exceed 1000 feet and this is so slightly related to the structure that it has been omitted. In the original drawings the horizontal scale was 4 miles to the inch and the vertical one-half mile to the inch. In the reductions for publication both are greatly reduced, but the ratio has been preserved. All sections are drawn and reproduced on the same scale. The sections are about one degree of latitude or 70 miles apart. The southern (No. 1) is in Tennessee and approximately on parallel 36° N., though lying obliquely across it. No. 2 in southern Kentucky, makes a small angle with parallel 37° N.; Nos. 3, 4 and 5 are respectively, essentially upon the next three parallels, while Nos. 6 and 7 are balanced obliquely, but not quite symmetrically on parallel 41° N. No. 6 is from northern Ohio, and No. 7 from northern Indiana. The sections were drawn from the four state geologic maps; Indiana on a scale of 4 miles to the inch, Ohio and Tennessee 8 miles to the inch, and Kentucky 12 miles to the inch. A contour map could be drawn on the Trenton if we had enough data. Well logs furnish excellent material if properly kept, and in most of Indiana and northern Ohio they are sufficient, but in other parts not yet available.

INTERPRETATION OF THE SECTIONS.

Section No. 1. Nashville Dome on the Anticline (Nashville Basin topographically) and this section cuts obliquely across it, N. W.–S. E. The anticline is here 120 miles across and 3,600 feet high. East dips average about 55 feet in a mile and west dips 50 feet.

Section No. 2. Intersects a sag in the crest, between the Nashville and Blue Grass basins or the Nashville and Jessamine domes. The structure is 140 miles wide and rises 2,100 feet on the west, but only 2,000 feet on the east. East dips are again steeper making this limb shorter. East dips average about 42 feet, west dips about 22 feet to the mile.

Section No. 3. Jessamine Dome. Width about 250 miles. Drillings show the Trenton limestone at Owensboro, near the west end of the section 3,500 feet below sea-level, and at eastern end of our section, about 3,300 feet below sea-level. Erosion has revealed the Trenton on the axis near Lexington with an altitude of 1,000 feet above sea level. Thus the structure along this line is 4,400 feet high. East dips are again much the steeper, averaging about 43 feet, and west dips about 31 feet.

Section No. 4. Crosses three states. About 35 miles in the central part is in Kentucky, while the eastern end is in Ohio and the western in Indiana. The structure here has a width of 215 miles and already shows the crest divided into two small swells, one east of Cincinnati and one west, with a sag of nearly 100 feet between them. Trenton rises in each crest to 50 or more feet above the river, showing at Patriot, Indiana, and Point Pleasant, in Ohio. The altitude attained here is essentially 3,000 feet, with dips a little stronger on the east side.

Section No. 5, A. & B. This section is divided into two parts at the Ohio-Indiana line, because it is so much longer than the others. It shows two axes clearly, one 30 miles east of the state boundary, and the other about 45 miles west. The sag between them is still very slight. The Ohio crest is 3,600 feet above the base of the eastern limb and the Wabash crest is about 2,600 feet above the western limb.

Section No. 6. Findlay dome on the east branch. The width here is 120 miles and the crest rises 2,800 feet above

the eastern limb and 1,300 feet, much more gently, above its western limb.

Section No. 7. Rensselaer dome on Wabash Arch. Section from South Bend, Ind., S. W. near Rensselaer, Remington, LaFayette and Rockville. The width is 150 miles at least and the altitude 1,600 feet, the least found anywhere.

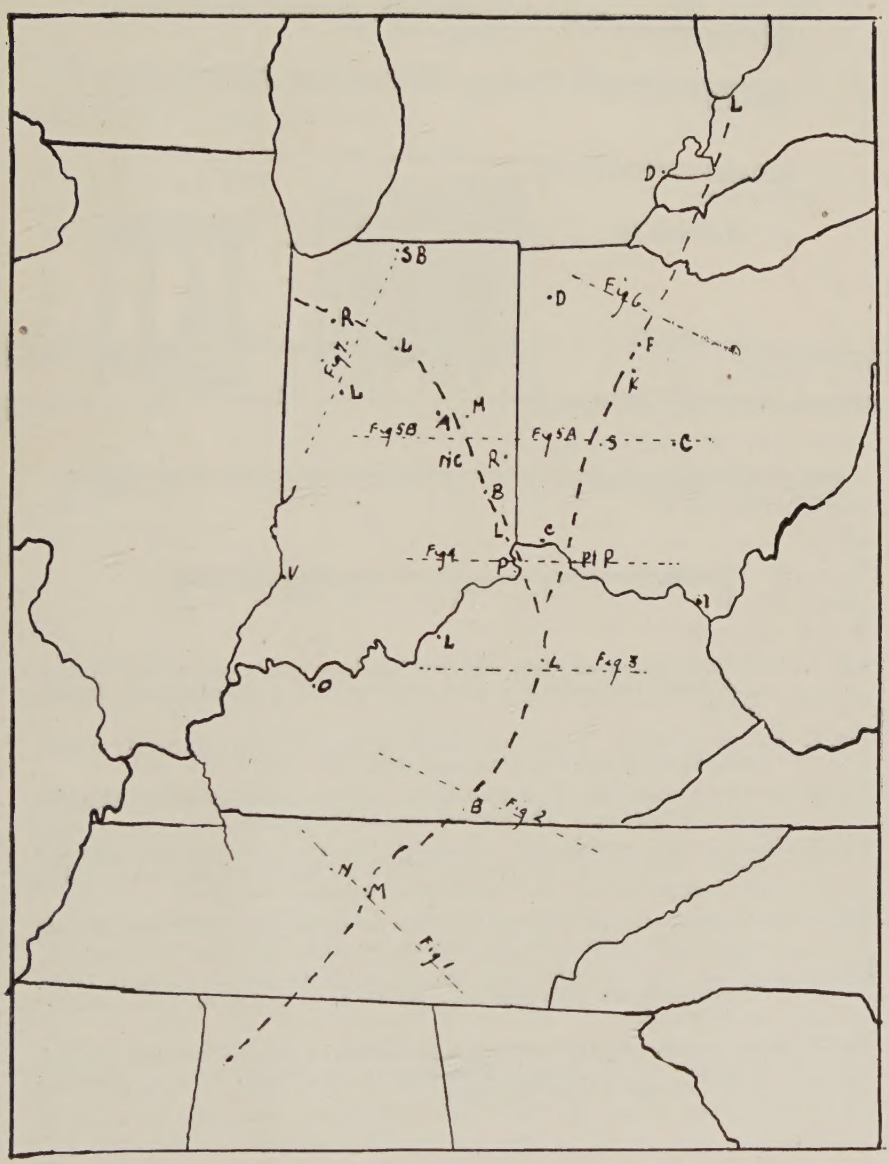
THE UNEVEN TOPPED CRESTS.

Another item of interest is the character of the crests of the Anticline. Beginning in the south and following the top of the Trenton limestone the figures may be given.

Murfreesboro, Tenn.	950±	feet	above	sea	level.
Burkesville, Ky.	250	"	"	"	"
Lexington, Ky.	1000	"	"	"	"
Patriot, Ky.	500±	"	"	"	"
Lawrenceburg, Ind.	158	"	"	"	"
Brookville, Ind.	174	"	"	"	"
Connersville, Ind.	117	"	"	"	"
Anderson, Ind.	66	"	"	"	"
Logansport, Ind.	334	"	below	"	"
Rensselaer, Ind.	158	"	"	"	"
Point Pleasant, O.	500±	"	above	"	"
Springfield, O.	450	"	below	"	"
Kenton, O.	500	"	"	"	"
Findlay, O.	340	"	"	"	"
Fostoria, O.	600	"	"	"	"

Still lower under Lake Erie.

Thus the crests are shown to be quite uneven topped, varying from 1,000— feet below sea level under western Lake Erie to 1,000 feet above near Lexington, Kentucky, and changing dip frequently along the axis. Dips along the axes however must be exceedingly small even compared with those on the flanks.



The group of states in which the Cincinnati Geanticline occurs. Heavy dashes show course of the main axes with branches; light dash lines show approximately the location of the seven sections. Dots with initial letters locate approximately most of the cities mentioned in the text.

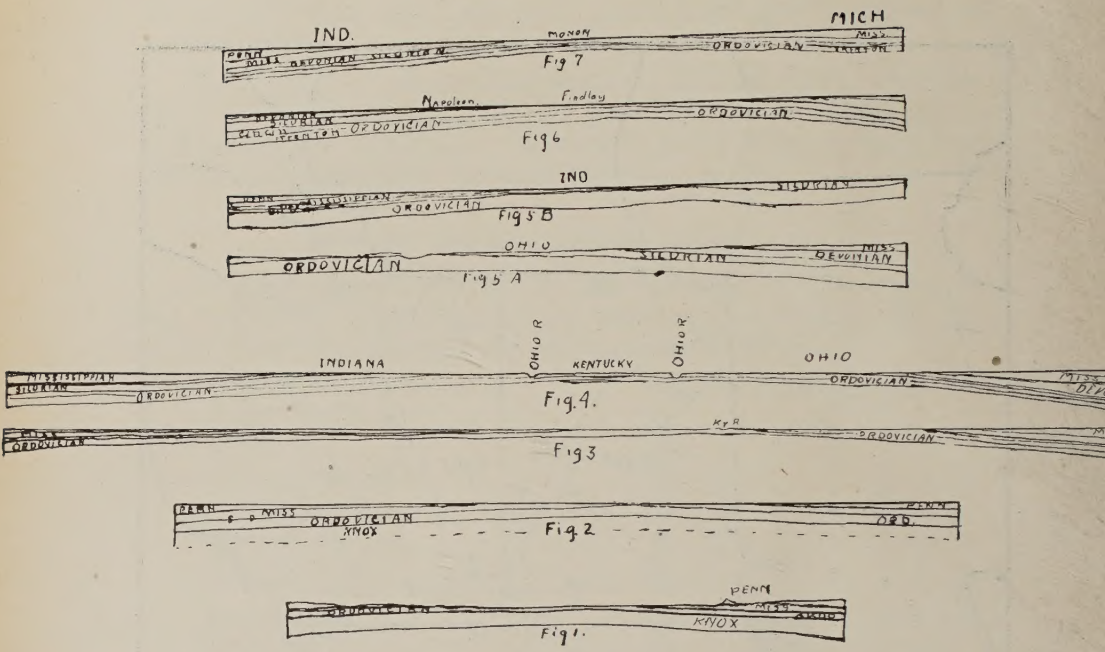


Fig. 1. Section in Tennessee basin with Murfreesboro nearly on the axis. Lower Ordovician corresponds roughly with lower Trenton of sections farther north.

Fig. 2. Structure section in southern Kentucky with Burkesville nearly on the axis. Silurian and Devonian very thin.

Fig. 3. Section through the Jessamine dome central Kentucky with Lexington near the axial line. The highest part of the anticline.

Fig. 4. Structure section along 39° N. parallel. The first section to show the two crests. Trenton is high enough to show in Ohio River on each crest but not high enough to show along river between crests.

Fig. 5. Divided into two parts, A in Ohio, B in Indiana. Two crests here 75 miles apart show clearly, one in Indiana, the other in Ohio.

Fig. 6. Structure section without all the detail across arch in northern Ohio. The three minor folds near the crest are too small to show on a section on this scale.

Fig. 7. Section nearly N-S in northern Indiana bearing same relation to Wabash Arch that No. 6 does to eastern branch. No. 6 and 7 are not continuous as No. 5A and 5B are. See Map.

(Date of publication, May 25, 1924.)